IDENTIFICATION, DISTRIBUTION, AND FAMILY PLACEMENT OF THE PLEUROCARPOUS MOSS BESTIA LONGIPES

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ABSTRACT

Recent field work and examination of specimens at CAS, MICH, MO, NY, SFSU, UBC and UC lead us to conclude that *Bestia longipes*, contrary to some earlier literature reports, is endemic to coastal regions of north-central to southern California. Based on analyses of DNA nucleotide sequence data we recognize *Bestia* in the Lembophyllaceae.

Key Words: Bestia, California, Isothecium, Lembophyllaceae, mosses.

Introduction

In examining the literature for Bestia longipes (Sullivant & Lesquereux) Brotherus, it becomes clear that this species endemic to the Pacific Coast of North America has been poorly understood. Part of this confusion can be attributed to various interpretations regarding the generic circumscription of Bestia and its taxonomic affinities at the family level (Lesquereux 1868; Lesquereux and James 1884; Grout 1928; Crum 1991). When first described in 1865 as Alsia longipes by Sullivant & Lesquereux, it became the third species in the genus Alsia (established by Sullivant in 1855) joining Alsia californica (W. J. Hooker & Arnott) Sullivant (transferred from Neckera) and Alsia abietina (W. J. Hooker) Sullivant (transferred from *Neckera*). The genus Alsia, with three species, was a morphologically heterogeneous assemblage of Pacific Coast endemics. Alsia abietina was recombined as *Dendroalsia abietina* in 1905 by Britton and Alsia longipes was transferred to Bestia in 1906 by Brotherus (Crosby et al. 2000). These three genera, each now monospecific, are today all placed in different families.

Had Brotherus (1906) retained *Bestia* as a monospecific genus, subsequent taxonomic and nomenclatural confusion would have been nil. However, this was not to be. Two other taxa (*Isothecium obtusatulum* Kindberg and *Thammium vancouveriense* Kindberg) were placed in *Bestia* by Brotherus (1925) further altering the generic

circumscription. Over the years Bestia has been attributed to such families as the Neckeraceae, Thamnobryaceae, Cryphaeaceae, Hypnaceae, Brachytheciaceae (Brotherus 1925; Crum 1987; Buck and Goffinet 2000; Crosby et al. 2000), and most recently, the Lembophyllaceae (Goffinet and Buck 2004; Huttunen et al. 2004; Quandt et al. 2008). This diversity of family placements was in part based on which species of Bestia had been critically examined and what combination of gametophytic and sporophytic characters were considered most important for inferring relationships. Grout (1928) also listed three species in Bestia. His interpretation of the genus included the incorporation of Hypnum brewerianum Lesquereux as a new combination within Bestia, expanding yet again the generic circumscription. Bestia breweriana (Lesquereux) Grout is now regarded as a synonym of Isothecium cristatum (Hampe) H. Robinson (Andrews 1952). The other species that Grout retained in Bestia he called B. holzingeri (Renauld & Cardot) Brotherus. This species also has a long nomenclatural history of being placed in 10 different genera containing 14 species synonyms (Norris and Enroth 1990). By the time Lawton (1971) published her moss flora of the Pacific Northwest it was generally known as Bestia vancouveriensis (Kindberg) Wijk & Margadant. Norris and Enroth (1990) resolved this part of the problem when they elevated Bestia vancouveriensis to generic rank as Bryolawtonia, and transferred it back to the Thamnobryaceae (Neckeraceae s.l.).

Crum (1987) and Norris and Enroth (1990) provided a detailed overview of this history and we will not repeat it further except to say that Crum (1987) proposed Bestia longipes be transferred to the Brachytheciaceae and viewed it to be closely related to Isothecium. Norris and Enroth (1990) also accepted this interpretation, as did Crosby et al. (2000). Crum (1991) further speculated that Bestia may not even need to be recognized as a monospecific genus at all, suggesting that B. longipes might be a mere form of Isothecium myosuroides Bridel. Recent DNA evidence supports the hypothesis that Bestia and Isothecium are indeed closely related (Goffinet and Buck 2004) yet distinct genera. Based on our herbarium studies and detailed examination of both gametophytic and sporophytic characters we conclude that Bestia is so distinctive as to require separate generic status. This conclusion is also supported by additional molecular data (Quandt et al. 2008).

DISCUSSION

Since the publication of a bryoflora of California (Norris and Shevock 2004a, b), a reexamination of material in California herbaria showed that several of the collections labeled and reported in the literature as Bestia longipes are in fact one or more species of *Isothecium*. Therefore, our earlier interpretation (Norris and Shevock 2004a) of this taxon was also clouded. This issue, however, became clear once we examined plants of Bestia longipes in the field from the general type locality in the Oakland Hills above Berkeley. Additional field work from coastal mountains in the San Francisco Bay region showed *Bestia* to be a rather common component of the flora on boulders along streams where it is often associated with Pterogonium gracile (Hedwig) Smith and species of *Isothecium*, primarily *I. cristatum*. This freshly collected material became the baseline for comparative purposes during our review of the herbarium record. While bryologists in California can attest to the difficulties in naming species of Isothecium many yet recognize the various growth form expressions that appear fairly constant in nature. The taxonomic and nomenclatural history of this genus has made working with Isothecium here in California, as well as more broadly along the Pacific Coast of North America, difficult and complex (Allen 1983). Despite the recent publication of two analyses based on molecular data (Ryall et al. 2005; Draper et al. 2007), consensus among west coast bryologists on the delimitation of *Isothe*cium taxa and what to call them remains elusive. Notwithstanding, knowledge about the appearance of Bestia in the field along with a sense of its very specific microhabitat renders it easily separated from *Isothecium*, even without sporophytes. One can recognize this very long-pendent, pinnately-branched moss by its branches being much shorter than the main axis. Smaller plants or those occurring in marginal habitat can have a main axis so short as to look more like an Isothecium. Dried Bestia upon close examination also looks different from Isothecium species, especially I. cristatum with its more julaceous branches, but it can superficially resemble I. myosuroides s.l. In the northern portion of its range, Bestia is considerably harder to distinguish in the field from I. myosuroides because Isothecium dominates the suitable habitat and plants from the two genera can be intertwined. We speculate that Isothecium, especially I. myosuroides, out competes and replaces Bestia for that particular ecological niche at the northern portion of its range.

The sporophytes of Bestia are not like the shorter generally asymmetrical 'hypnaceous' capsules of Isothecium. However, the perichaetial leaves in both Bestia and Isothecium are greatly enlarged and sheathe the seta base. Developing sporophytes in *Bestia* with light colored setae are inserted ventrally on the main stem axis adjacent to the substratum. Because they are oriented upward along and parallel to the main stem axis, they can be easily overlooked during a casual inspection of plants in the field. We found the illustration of Bestia longipes (as Alsia l., plate 63) in Sullivant (1874) and reprinted in part (Brotherus 1925) to be remarkably detailed and accurate. Isothecium cristatum on the other hand is commonly associated with Bestia especially in the central portion of its range and generally produces abundant sporophytes with reddish setae that are erect and easily visible above the branches. When hydrated, Bestia has a rather plumose appearance and cascades downward from the substrate. Colonies can cover square meters of rock surface.

The following key should readily separate *Bestia* from *Isothecium* species.

- 1b. Leaves with serrulations extending from leaf apex to middle or even lower, at least some teeth composed of more than one cell; cells across leaf with an abrupt transition from the green alar region to a paler green throughout rest of leaf; costa prominent, extending rarely beyond 2/3 of leaf, ending in 1 to few spines;

juxtacostal region with elongate cells (up to 8:1) and much longer than cells at leaf apex; foliose pseudoparaphyllia irregularly lobed or toothed with elongate cells making up those teeth; capsules oblong-ovoid, suberect to cernuous, generally slightly asymmetrical with an abrupt constriction below mouth... Isothecium

DISTRIBUTION

After examining collections labeled *Bestia* from several herbaria we conclude that this monospecific genus is a Californian endemic and confirmed for the following counties: Alameda, Contra Costa, Lake, Los Angeles, Marin, Mendocino, Monterey, Napa, San Benito, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, Sonoma, and Ventura. The only coastal county within this range lacking Bestia is San Francisco, due to a lack of suitable riparian habitat (Shevock and Toren 2001). Although Bestia longipes was not encountered during our herbarium review as occurring in Orange and San Diego counties just south of Los Angeles County, we believe there is a high probability that *Bestia* will be discovered in this area because seemingly appropriate habitats occur in the coastal portions of the Peninsular Ranges. Moreover, the range of Bestia could perhaps extend yet farther south to Guadalupe Island, Baja California, Mexico where both Alsia and Dendroalsia reach their southernmost outposts (Schofield 2004).

Reports of *Bestia* (Norris and Shevock 2004a) from the northwest corner of California in Del Norte, Humboldt, Shasta, Siskiyou counties and the northern Sierra Nevada in Placer County are erroneous and represent Isothecium species. Two Oregon specimens identified as *Bestia* (NY) and cited in Chapman and Sanborn (1941) also proved to be Isothecium. Bestia longipes was not reported from Oregon by Christy et al. (1982) or Lawton (1971). Koch (1950) reported Bestia for Oregon although no specimen was cited. Two historical specimens, correctly identified as *Bestia longipes*, are attributed to Alaska and seem to be distributional anomalies. The specimen housed at NY was purchased sometime in the late 1800s. It lacks data except for being attributed to Alaska. The other collection (originally at CAS but now at UBC) states "collected by Kellogg in 1867 from Redout Bay, Alaska." However, in both cases these historical collections seem geographically unlikely to have been collected in Alaska. Also, both of these packets have no soil, litter or other mosses mixed with the specimen, but rather, just a few 'clean' individual branches. We view these two collections as likely some type of herbarium processing error. Also, Bestia (as Alsia longipes) was not reported from Alaska by Cardot and Thériot (1902, 1906). Considering the level of bryophyte collecting in the coastal portions of the Pacific Northwest from Alaska,

British Columbia, Washington and Oregon over the past century without encountering a modernday collection of *Bestia longipes* leads us to conclude that it is in fact a Californian endemic.

Bestia is most commonly encountered at sites with cool air drainage patterns and is therefore more or less restricted to narrow stream channels and canyons. Although Bestia prefers rock walls and massive boulders in partial shade, it can also infrequently occur on adjacent bases of tree trunks, primarily Umbellularia californica (Hooker & Arnott) Nuttall. Many of the habitats of Bestia are influenced by summer fog and cooler temperatures compared to hotter inland valleys. The elevation range is from 50–2500 ft.

SPECIMENS EXAMINED

CALIFORNIA. Alameda Co.: Alameda, Gibbons 14 (NY); San Antonio Creek, Kellogg s.n. (NY); Oakland, collector unknown (MO, NY); Oakland, Eaton s.n. (NY); Berkeley, Howe 27 (MO, NY, UBC) & 232 (CAS, MICH, NY, UC); Strawberry Creek east of Hilgard Hall, U.C. Berkeley, Norris 82503 (CAS, UC); Garin Regional Park southeast of Hayward, Whittemore 5295 (CAS, MO, UC); Grass Valley Creek, Anthony Chabot Regional Park, Shevock 29365 (CAS, COLO, H, MO, NY, S, UC, US) & 29485 (CAS, KRAM, MO, NY, UC). Contra Costa Co.: Gorge Trail toward Lake Anza, Tilden Regional Park, Norris 109512 (CAS, COLO, DUKE, H, MO, NY, OSU, UBC, UC, UNAM, UNLV, US) and Norris 109518 (UC); Havey's Canyon Trail, Wildcat Canyon Regional Park, Norris & Hillyard 109589 (CAS, MO, UC); Castle Rock Park, Schofield 87551 (MO, UBC); East Fork Sycamore Creek, Mt. Diablo State Park, Shevock & Ertter 24528 (CAS, US) and Shevock & Ertter 24531 (CAS, DUKE, E, H, UC). Lake Co.: Anderson Springs, Toren 2529 (SFSU); southern shore of Clear Lake at Kelsey Creek Slough, Clear Lake State Park, Toren 6844 (CAS); Troutdale Creek, Mt. St. Helena, Robert Louis Stevenson State Park, Toren 8427 (CAS). Los Angeles Co.: near Pasadena, McClatchie 486 (NY); Monrovia Canyon, collector unknown (NY); San Gabriel Mts., McClatchie s.n. (UBC); White's Landing, 5 mi north of Avalon, Santa Catalina Island, Steere s.n. (UBC). Marin Co.: Mill Valley, *Blasdale s.n.* (CAS, UBC, UC); Devils Gulch, Samuel P. Taylor State Park, Shevock 29824 (CAS, H, S, UC); Panoramic Drive, Mt. Tamalpais State Park, Shevock 29833 (CAS, DUKE, E, MO, NY, UC, US). Mendocino Co.: no locality given beyond county, Toren & Showers s.n. (CAS); Hendy Woods State Park, Toren 2772 (SFSU); Parsons Creek below Huntley Peak, Heise 2230 (UC). Monterey Co.: divide 0.5 mi south of Santa Lucia Memorial Park, Los Padres National Forest, Shevock & Kellman

24811 (CAS, MO, UC); Alder Creek Campground, Los Padres National Forest, Shevock & Kellman 27729 (CAS, UC); Indians Road 4.52 mi north of Fort Hunter Liggett Military Reservation boundary, Los Padres National Forest, Kellman & Shevock 3602 (CAS); South Fork Devils Canyon Creek below Canogas Falls, Los Padres National Forest, Shevock & Kellman 27830 (CAS, MO, NY); Palisades off of Gabilan Road, Fort Hunter Liggett Military Reservation, Kellman, Shevock, & Robertson 3743 (CAS); Big Sur River, Kellman 3996 & 4000 (CAS); Little Sur River below Jackson Camp, Los Padres National Forest, Shevock & Kellman 29054 (CAS, MO, NY) and Kellman & Shevock 4873 (CAS); Big Creek, UC Landels-Hill Big Creek Reserve, Shevock & Kellman 28898 (CAS, UC) and Devil's Creek at Redwood Camp, Shevock & Kellman 27759 & 27842 (CAS, MO, NY, UC) and Shevock & Kellman 27765 (CAS, MO, NY), Kellman & Shevock 4909, 5016 (CAS); South Fork McWay Canyon, Julia Pfeiffer Burns State Park, Kellman 4946 (CAS); Rocky Ridge Trail to Soberanes Creek, Garrapata State Park, Kellman 3358 (CAS); Grimes Canyon below highway 1, Shevock & Kellman 27739 (CAS, UC); Redwood Gulch along highway 1, Becking 670719 (UBC); 1 mi south of Castro Canyon, Schofield 29181 (UBC). Napa Co.: St. Helena Creek, highway 29 at milepost marker 47.62 about 1 mi south of Lake County line, Shevock 29852 (CAS, COLO, DUKE, H, KRAM, MO, NICH, NY, OSU, UC, UNAM, US, WTU). San Benito Co.: Juniper Canyon along stream, Pinnacles National Monument, Kellman, Shevock, & Villaseñor 4244 & 4251 (CAS). San Luis Obispo Co.: Cypress Mountain Road southern end of Santa Lucia Range, Carter 1325 (UC); Cerro Alto Trail, Cerro Alto Campground, Los Padres National Forest, Carter 1843 (UC). San Mateo Co.: Pescadero Creek about 3 mi west of San Mateo Park entrance, Pescadero Road, Schofield 11206 (MICH, MO, NY, UBC, UC) & 96269 (MO, NY); Purissima Creek near Searsville Lake, Schofield 12899 (MO, NY, UBC, UC) and Steere s.n. (UBC); Lake Pilarcitos, Koch 3366 (MICH, NY, UC); Highway 1, about 2 mi north of Santa Cruz County line, Koch 2083 (MICH, NY, UC); between Serpentine Trail and Sylvan Trail, Edgewood County Park, Whittemore & Sommers 5238 (CAS) and 5240 (MO); Sylvan Way, Redwood City, Whittemore 3114 (CAS) and 1407 (MO); San Mateo Creek, Howe s.n. (NY); Tafoni Sandstone Formation, El Corte de Madera Creek Open Space Preserve, Shevock 29927 (CAS, COLO, DUKE, E, GOET, H, KRAM, MA, MHA, MICH, MO, NICH, NY, OSU, PE, S, UBC, UC, UNAM, US). Santa Barbara Co.: above Santa Barbara, Smith King s.n. (UC); Cold Springs, Los Padres National Forest, Shevock 27875 (CAS, MO, NY, UC) and

Laeger 526 (CAS); Pelican Bay, Santa Cruz Island, Fosberg 208 (UC); Lady's Harbor, Santa Cruz Island, Fosberg 361 (NY); Cherry Canyon, Santa Rosa Island, Channel Islands National Park, Shevock 20911 (CAS, UC) and Water Canyon east of Black Mountain, Santa Rosa Island, Channel Islands National Park, Shevock & Rodriguez 20817 (CAS, UC). Santa Clara Co.: Alum Rock Canyon, San Jose, Bradshaw 496 (CAS, MICH, NY, UBC, UC); Alum Rock Park, Schofield & Mueller 6923 (MO) & 36446 (UBC); Lower Braen Canyon and Hunting Hollow east of Gilroy Hot Springs Road, Henry W. Coe State Park, Whittemore & Briggs 6745 (CAS, MO, NY) and canyon at Woodchopper Creek, Whittemore & Briggs 6766 (CAS, MO, NY); Woods Trail from Mt. Umunhum Road near Guadalupe Creek, Sierra Azul Open Space Preserve, Whittemore et al. 6105 (CAS, MO); Mine Hill Trail adjacent to new Almaden Trail, Almaden Quicksilver County Park, Whittemore 5323 (CAS, MICH, MO); Mt. Hamilton Road at milepost 8.5, entrance to Joseph D. Grant County Park, Whittemore 6058 (CAS, NY) & 6056 (MO); Jasper Ridge Nature Reserve, Stanford University, Schofield & Thomas 71538 (MO, UBC) and 96794 (MO, UBC); New Grade Road, Geis 657 (MICH); Stevens Canyon Creek above reservoir, Steere s.n. (UBC); Los Altos Hills, Schofield 23051, 63731, & 112008 (UBC). Santa Cruz Co.: Granite Creek, Kellman 1105 (CAS, UC); Laguna Creek, Kellman 1854 (CAS); Baldwin Creek, Wilder Ranch State Park, Kellman 832 & 2579 (CAS); Majors Creek Canyon near Highway 1 between Santa Cruz and Davenport, Kellman 1065 (CAS); Scott Creek, Swanton Road and milepost 4.15, Kellman 410 (CAS); confluence of Boyer and Big Creek, Kellman 1897 (CAS); Zayante Canyon Road north of Felton, Norris 86869 (UC). Sonoma Co.: Adobe Canyon near Kenwood, Koch 463 (MICH, NY, UC); Sugarloaf Ridge State Park, Norris & Hillyard 109804, 109812, & 109814 (CAS, UC); Fife Creek, Armstrong Redwoods State Reserve, Shevock 29859 (CAS, DUKE, MO, NY, UC); Audubon Canyon Ranch Bouverie Preserve north of Sonoma, Carter 1874 (UC). Ventura Co.: Willard Canyon, McClatchie s.n. (NY); Carlisle Creek, Santa Monica Mountains., Wishner & Sagar 2005-09-23-1 (CAS, UC); Big Sycamore Canyon, Santa Monica Mountains., Point Mugu State Park, Sagar 711 (UC).

FAMILY PLACEMENT

As mentioned previously, components within *Bestia* have been assigned to a wide assortment of moss families since the late 1800s. Crum (1987) aligned *Bestia longipes* in the Brachytheciaceae and this placement was generally accepted by other bryologists (Crosby et al. 2000). DNA-

based analyses, however, suggest that *Bestia*, along with *Isothecium*, belong in the Lembophyllaceae (Goffinet and Buck 2004; Huttunen et al. 2004; Tangney 2007; Quandt et al. 2008). As part of our present review of the problem, we obtained a sequence for the plastid *rps*4 gene from a recent collection of *B. longipes* and found that sequence nearly identical to a sample included in earlier analyses. The DNA evidence from both collections place *Bestia longipes* into a clade that includes other genera generally attributed to the Lembophyllaceae, corroborating earlier conclusions. Therefore, we view *Bestia* and *Isothecium* as the two North American representatives of the Lembophyllaceae.

RARITY AND CONSERVATION IMPLICATIONS

Although Bestia is an endemic monospecific genus restricted to coastal California, it is not now of conservation concern. Populations of Bestia are relatively small within a narrow band of suitable habitat but occurrences are numerous and geographically dispersed in the state. Riparian areas also generally have layers of legal protections at both the state and federal levels, especially along those streams that contribute spawning habitat for anadromous fisheries. Bestia occurs on a wide variety of public lands from county and regional parks to state parks, national forests and national parks thus contributing to its long-term conservation. Additional populations of Bestia are likely to be documented with ongoing exploration and collection within the range of this species. We suspect that populations have been overlooked when Bestia is inadvertently assumed to be *Isothecium* in the field, and therefore, it is probably under-collect-

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REVIEW

Flora of China Illustrations. Vol. 22. Poaceae. By Wu Zhengyi, Peter H. Raven (editorial committee co-chairs), Hong Deyuan (editorial committee vice co-chair). 2007. Science Press (Beijing, China) and Missouri Botanical Garden Press (St. Louis, MO). 937 pp. Hardcover. \$140.00. ISBN 978-1-930723-61-0.

China harbors an incredible diversity of plants, including ca. 31,000 fern and seed plant species, or one-eighth of the world's vascular flora. By comparison, the United States and Canada—together twice the size of China in land area—have one-third fewer species (ca. 20,000). There are ca. 1,800 grass (Poaceae) species in China, including 534 species of woody bamboos.

Flora Reipublicae Popularis Sinicae (FRPS), a Chinese-language Flora of the country, was published as 80 volumes in 125 books from 1959 until its completion in 2004. The Flora of China (FOC) is an English-language revision of FRPS that will comprise 49 volumes when complete, including 24 volumes devoted to illustrations. As of December 2008, 16 text volumes and 14 illustrations volumes had been published, the first in 1994. The Poaceae text volume was published in 2006.

The FOC is unusual in having separate text and illustrations volumes. Unfortunately, for the Poaceae (and perhaps all) treatments, the text volume does not reference figures in the illustrations volume, which means that the user cannot tell from the text volume if a species is illustrated in the companion volume nor, if it is illustrated, on what page the figure appears. Because the genera in both volumes are arranged by tribe, not alphabetically, the index in the illustrations

volume must be consulted to find out if a species is figured, and on what page.

All of China's 226 grass genera (including native and naturalized species and economically important exotics) in 28 tribes are illustrated and arranged as in the text volume, beginning with Bambuseae and ending with Andropogoneae. Seventy-one percent (1,271) of the species and 74 infraspecific taxa are illustrated as line drawings in 904 full-page plates, and a lovely color figure of *Phyllostachys reticulata* serves as the frontispiece. Indeed, all of the line drawings, inked by 76 illustrators, are beautiful and detailed. Most were published previously in FRPS, although many of these were redrawn for FOC. Text in the plates is minimal—only scale bars, which are given for about half of the plates, and numbers identifying the figure parts which are explained in the captions. The captions also include the scientific, Chinese, and pinyin names of the taxa, page references to where the taxa are treated in the FOC Poaceae text volume and FRPS, the names of the artists, and the sources of illustrations not published in FRPS. There are three indices of names—Chinese, pinyin, and scientific.

The Poaceae illustrations volume is a vital companion to the text volume for those learning and identifying Chinese grasses. In fact, as one-sixth of the world's grass species are found in China, both volumes should be close at hand for anyone interested in the diversity of this large, ecologically and economically important plant family.

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